

PREDATION OF *ANETIA BRIAREA* GODART
(NYMPHALIDAE: DANAINAE) AT AGGREGATION SITES:
A POTENTIAL THREAT TO THE SURVIVAL OF A RARE
MONTANE BUTTERFLY IN THE DOMINICAN REPUBLIC

DEREK S. SIKES AND MICHAEL A. IVIE

Department of Entomology, Montana State University, Bozeman, Montana 59717, USA

ABSTRACT. Evidence of predation on *Anetia briarea* was discovered at the single known aggregation site on Pico Duarte in the Dominican Republic. In addition to birds, feral rats (*Rattus rattus* L.) are hypothesized to be involved in predatory activity affecting the aggregation. Analyses show no biases in the sex, size, or color of *A. briarea* taken as prey. Steps that can be taken to protect the aggregating butterflies include removal of exotic rats from the colony area.

RESUMEN. Evidencia de predación de *Anetia briarea* fue descubierta en el único sitio conocido de agregación en Pico Duarte en la República Dominicana. Además de pájaros, se cree que ratas (*Rattus rattus*), están involucradas en la predación de las colonias. Un análisis de predación de las colonias de *A. briarea* muestra no tendencia por el género, tamaño, o color de la presa. Actividades para proteger las mariposas que se están agregando incluyen la eliminación de las ratas extrañas del sitio de agregación.

Additional key words: rats, conservation biology, West Indies.

Predation on butterflies, although thought to be important evolutionarily, is rarely observed in the field (Brown & Vasconcellos 1976, Bowers et al. 1985, Brower & Calvert 1985). With the exception of the observations documenting predation of monarchs at overwintering sites (Brower & Calvert 1985, Sakai 1994) most of our knowledge regarding predation on butterflies is obtained indirectly by analysis of the evidence of predation, such as beak-marked (e.g. Shapiro 1974, Smith 1979) or tooth-marked (e.g. Brower et al. 1985) wings. Laboratory investigators, studying the acceptability of various butterflies to vertebrate predators, have found great variation in palatability within and between butterfly species (e.g. Brower & Brower 1964, Duffey 1970, Bowers 1980, Brower 1984).

Anetia briarea Godart (Nymphalidae) is a rare montane danaine butterfly of the Greater Antilles (Riley 1975, Schwartz 1989, Alayo & Hernadez 1987, Vane-Wright et al. 1992, Smith et al. 1994). It shares with several other danaines the characteristic of forming seasonal aggregations, often at high altitudes (e.g., species of *Anetia*, *Euploea*, *Tirumala*, *Ideopsis*, *Salatura*, *Parantica*, and *Danaus*) (Brower et al. 1977, Ivie et al. 1990, Wang & Emmel 1990, Llorente-Bousquets et al. 1993). However, in sharp contrast to such common species as the monarch (*Danaus plexippus* L.), with colonies estimated to number up to 20 million individuals (Brower & Calvert 1985), and *Danaus genutia* (Cramer) and *Euploea* spp. with colonies of up to 50 thousand (Wang

& Emmel 1990, Ishii & Matsuka 1990), the only known colony of *A. briarea* contains a mere 500–2,500 individuals (Ivie & Sikes unpublished data). Even such a small aggregation potentially offers a rich concentration of resources for predators.

The exact role of seasonal aggregation is not well understood in *A. briarea*, but since aggregations occur yearly at the same sites (Ivie & Sikes unpublished data), it is currently assumed to be an obligate life history trait. The monarch butterfly maintains large populations in temperate habitats by withdrawing to an amenable climate and diapausing in aggregations during the winter (Calvert et al. 1989). Migrations by *A. briarea* seem to be related to wet/dry cycles, and we expect that they are comparatively local in extent. In any case, such high densities in an exposed setting would be expected to require the butterflies to have evolved some type of predator deterrent (Vulinec 1990).

This hypothesis has only been tested with one of the aggregating danaine species, the monarch butterfly. This species is somewhat protected from predation by sequestered cardiac glycosides obtained from asclepiadaceous larval host-plants, although individual bird and mammal predators sometimes overcome this defense (Fink & Brower 1981, Brower & Calvert 1985, Brower et al. 1985, Sakai 1994). Although the Hispaniolan host-plant of *A. briarea* remains unknown, Brower et al. (1992) recently have reared *A. briarea* larvae on Floridian *Cynanchum angustifolium* (Pers.) (Asclepiadaceae), and spectrophotometric analysis of wild collected *A. briarea* adults shows they contain small quantities of cardenolides (L.P. Brower, M.A. Ivie, A. Alonso & D.S. Sikes unpublished data). However, during visits to the only known *A. briarea* aggregation site in July and August 1992 and July 1993, evidence of predation was found in the form of beak and tooth marks on living individuals and discarded wings. These findings mirror those of Brower and Calvert (1985) on the Mexican monarch.

METHODS

Observations were made during visits to the 2670 m aggregation site described by Ivie et al. (1990), in July and August 1992 and July 1993. During the daylight and crepuscular hours of 25–29 July 1993, the colonies were monitored for evidence of predation.

To investigate the incidence of bird predation attempts, we collected a subsample of 78 butterflies from a sample of 195 (with a bias towards individuals with undamaged wings) on 8 July 1992. Another sample (lacking bias) of 179 individuals was taken and released on 28 July 1993. Each sample was from a single cluster of butterflies occupying

one branch (see Ivie et al. 1990), and data were collected as an adjunct to sex-ratio studies. The individuals from these two samples were scored for bird beak-marks, and analyzed following procedures outlined by Shapiro (1974).

To examine sex, size, and coloration as predictors of beak-marking [which may affect predation bias (Smith 1979, Bowers et al. 1985)], data from the July 1992 sample were analyzed using SAS, release 6.08, (SAS 1990). Both parametric (ANOVA) and non parametric (Chi², Mann-Whitney) analyses were performed.

We found seven middens of "shucked" wings left below clusters by one or more predators on 26 August 1992, and considered them to be evidence of successful predation (Fig. 1, 2). Damage to the wings (Figs. 3-5) was consistent with small mammal tooth marks observed by Brower et al. (1985). Lincoln Brower examined the wings, and agreed with this interpretation (L.P. Brower, pers. comm.). The middens were photographed and collected for analysis. The wings from each group were then scored for wing-type (e.g. right-front, etc.) and counted. A minimum number of individuals represented in each group was determined by the maximum occurrence of a wing-type. For example, if there were 8 right-fore wings in a midden, and less than 8 of the 3 other types, then 8 would be the minimum number of individuals represented.

RESULTS

Of the 78 live butterflies taken 8 July 1992 (and selected for relatively intact specimens), 32 (41%) showed distinct beak-marks and an additional 22 (28%) showed indistinct marks that may have been made by birds. This sample did not show a significant difference between the damaged wing frequencies on males versus females ($\text{Chi}^2=0.28$, $df=1$, $P>0.50$), although we found the wing length of females to be greater than that of males (45.8 ± 1.8 mm, $n=38$ vs. 44.2 ± 1.4 mm, $n=40$; Mann-Whitney $S=1902.5$, $Z=4.00$, $P=0.0001$). No significant differences were found between the mean lengths of damaged versus undamaged wings, both between and within sexes, nor did we find a difference between the damage frequencies of darker morphs versus lighter morphs (ANOVA, all $P>0.05$).

The 28 July 1993 sample of 179 live individuals showed distinct beak marks on 84 (47%) specimens and indistinct marks on 13 (7%). The ratio of beak-marked males ($n=88$) to females ($n=91$) did not differ significantly from 1:1 ($\text{Chi}^2=0.135$, $df=1$, $P>0.50$). Because these specimens were released or held for life history studies, to minimize handling, color-morph and size were not recorded.

Of the seven middens of disembodied wings found beneath clusters, two were ca. 60 cm apart beneath a cluster and the other five, also



Figs. 1-2. Middens of *Anetia briarea* wings found beneath colonies on Pico Duarte, Dominican Republic.

within 60 cm of each other, were found beneath clusters located in a different tree. The seven middens contained 16, 8, 19, 23, 40, 26, and 32 wings. These wings were determined to represent the consumption of at least 47 (4, 2, 7, 7, 11, 8, 8) butterflies.

The total aggregation documented during August consisted of six clusters in four trees, with an estimated total population size of 2000–2500 individuals. The individuals consumed by the predator that made the middens thus represent a ca. 2% mortality to the aggregation.

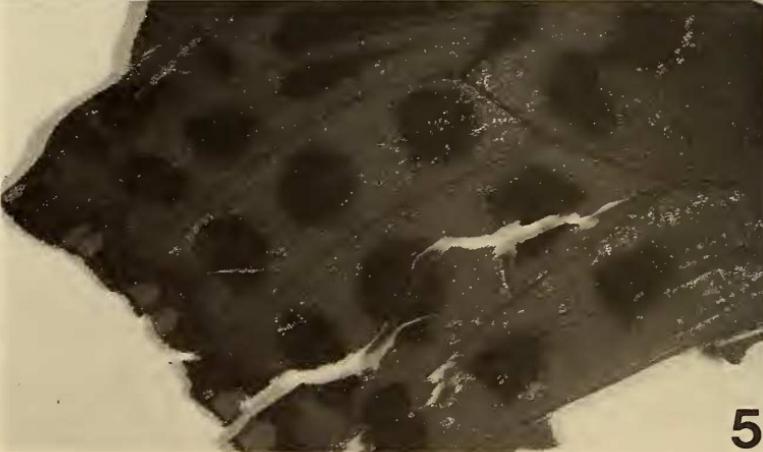
Predator surveys at the aggregation site on 25–29 July 1993 provided few suspects. Two bird species occasionally vocalized in the vicinity, but no birds were seen close to the butterflies. A single *Anolis* sp. was observed on the ground in the area, but seemed too small (ca. 5 cm snout-vent length) to account for the *Anetia* predation. Although bats may be present near or at the site, observations made during crepuscular hours revealed no evidence of bats. In addition, because the piles of wings were 3–5 meters below the branches, bats probably did not make the middens. Bats dropping butterfly wings from feeding roosts in the branches above would produce a dispersed refuse area, not the tight groups observed (Figs. 1, 2).

Lastly, DSS observed an individual of the introduced rat, *Rattus rattus* L., at the site on 28 July 1993. Since the marks on the wings are consistent with small mammal attacks, and since no other small ground-dwelling predacious mammal is known to be present in the area, the evidence points toward *Rattus rattus*.

DISCUSSION

Smith (1979) investigated beak-marks on the wings of an African population of *Danaus chrysippus* (L.). He concluded that larger individuals of both sexes were more frequently beak-marked. Bowers et al. (1985) found that birds attacked more females than males of the checkerspot butterfly, *Euphydryas chalcedona*, but the effect of prey size was not investigated. Brower and Calvert (1985) found the opposite for aggregating monarchs, with birds selecting for the more palatable males in a population without significant sexual dimorphism in prey size. Sakai (1994), reported that predatory birds preying on monarchs at a California overwintering site showed no preference for the sex of prey. In agreement with Sakai's findings on monarchs, our data showed no patterns of preference by birds for sex, size, or color of *A. briarea*. This may be due to a lack of obvious sexual dimorphism and predicts no difference in palatability between the sexes.

Brower and Calvert (1985) reported high predation on the colonies of *D. plexippus* in Mexico by birds and mammals. They conservatively calculated a 9% annual mortality from predation at the colonies. At a



California monarch overwintering site Bell and Dayton (1986) reported a range of 0.345–2.21% annual mortality due to chestnut-backed chickadees. Sakai (1994), also working at a monarch overwintering site in California, documented an estimated annual mortality of 6.51–7.43% due to a single pair of rufous-sided towhees. Our conservative estimate of 2% annual mortality for 1993 falls within these estimates.

Predation on aggregating monarchs is spatially divided into those taken from the arboreal clusters by birds and those taken by mice and voles from fallen groups on the ground below the clusters. This is consistent with observations of *A. briarea*. Those individuals with evidence of attempted bird predation (i.e. beak-marked wings) were found within arboreal clusters, while the suspected rat predated individuals were found in piles below. These later individuals must have been “shucked” on the ground or the disembodied wings would have dispersed as they fell from the branches, thus not forming the tightly clumped middens we observed. Sakai (1994) reported middens created by birds dropping remains from perches. However, the middens he observed consisted of the remains of only a single butterfly, generally with four wings per midden and numerous middens scattered beneath perches.

Clumps of monarch butterflies may fall to the ground due to low temperatures (Masters et al. 1988), lipid depletion (Brower & Calvert 1985), wind, or heavy precipitation (Calvert et al. 1983). Many *A. briarea* were observed in July 1992 that had been knocked to the ground by a heavy hail storm (M.A. & R.O. Ivie unpublished data). Our guides reported hail to be common in the area.

We suspect that the piles were formed by cold temperatures or precipitation having knocked groups of *A. briarea* from the clusters and rats found them before they could warm up to escape. This is further supported by wing damage consistent with small mammal feeding on the piled wings (L.P. Brower pers. comm., Figs. 3–5).

The introduced, anthropophilous, omnivorous, and aggressively colonizing *Rattus rattus* may have only recently reached this area. Hispaniola has perhaps the longest history of European rat infestation in the New World. An archeological dig at Christopher Columbus's alleged first encampment in the New World (La Navidad, occupied 1492–1493 in



FIGS. 3–5. Examples of wings from middens showing wing damage hypothesized to be caused by *Rattus rattus* feeding on *Anetia briarea*. Note the parallel scratches/tears on the wings.

what is now Haiti) yielded the jaw of a black rat (*R. rattus*) dated to pre-1510 (Deagan 1987, Deagan 1988, Wing 1989). However, its presence at high elevations may be tied to human disturbances, which have only recently been important in the Pico Duarte area. In 1988 we saw no rats at the Park cabin, La Compartación, located at 2290 m and an hour's hike below the aggregation site, nor in the area above the cabin. However, by 1992, rats were present at La Compartación, and in 1993 they were obnoxiously abundant. In recent years, the cabin has hosted hundreds of tourists annually, mostly in the winter months, and hundreds of overflow tourists camp above the aggregations in El Vallecito de Lilis (Zanoni 1990). The transport of foodstuffs and gear afford the opportunity for rats to reach the uninhabited aggregation site, and the accumulated refuse at the cabin provides an excellent rat habitat. Feral populations can then spread from these human-use sites. In an analogous situation, introduced rats which have wiped out populations of lowland insects in New Zealand have had little success in invading uninhabited high elevation zones (Watt 1979). The increase in tourism, and the accompanying disturbances on Pico Duarte may have only recently created an opportunity for rat invasions into the area.

Ideally, data on abundance, diet, and local ecology of rats at the aggregation sites should be collected before raising an alarm about their potential impact. However, we lacked the necessary traps and other equipment to do such a study, and other constraints preclude returning to conduct such a study in the near future. Due to the small population size of the only known aggregation of this extremely rare and poorly known butterfly (see Ackery & Vane-Wright 1984, Ivie et al. 1990, Brower et al. 1992), the knowledge that the aggregation is subject to predation is important. The incidence of predation by native birds, bats and lizards can be considered a normal part of the biology of the species, but we hypothesize that rat predation is a new and dangerous escalation. If *Rattus rattus* has no aversion to the defense evolved in response to the few native predators, the future of the colonies may be in danger.

Introduced rats have a long history of negative impact on island species (Day 1981, King 1984, Howarth & Ramsay 1991). The extinction of numerous species of birds, tortoises, mammals and an iguana have been blamed, at least in part, on feral rats which gained access to islands via European sailing ships (Day 1981). Paramonov (1958, 1963) reports that rats caused the extinction of a phasmid (Orthoptera) on Lord Howe Is., and Watt (1979, see also Moffett 1991) implicates them in the expatriation of wetas (Orthoptera, *Deinacrida*) and other insects from historic range in New Zealand. Kuschel (1987) reported the discovery of the remains of three weevil species in New Zealand, that he posits were made extinct by the Polynesian rat. To our knowledge, this study

is the first report of a New World insect species being impacted by Old World rats.

The rapid human population growth and consequent destruction of native habitat on the island of Hispaniola (Kurlansky 1992) threaten to impact the survival of *A. briarea*. Although the aggregations are protected by their remote location in the Parque Nacional Armando Bermudez, the butterflies leave the aggregations to fly to areas lower on the mountain (Schwartz 1989, MAI and DSS pers. obser.). These mid-elevation areas are increasingly cultivated for export crops of vegetables and fresh flowers. The pesticide loads associated with export-quality requirements are bound to be detrimental to non-target species such as *A. briarea*. Any additional pressure on this species could place it in danger of extinction, and we feel the presence of rats at the aggregation site is cause for alarm. Eradication of rats from the mountain, discovery of and protection of other *Anetia* aggregation sites, if they exist, and the location of and protection of host-plant stands, should be made a high priority. The conservation of this species need not become a rescue situation if appropriate measures are taken now.

ACKNOWLEDGMENTS

Several people and agencies provided help that made this work possible. The assistance and hospitality of J. and M. Brodzinsky in Santo Domingo was greatly appreciated. We are indebted to those who assisted us in the field: R. P. Rosenfeld, R. O. Ivie, T. McDowell, K. A. Guerrero, and the guides V. Peralta and C. Canelas. We thank L. P. Brower for sharing his knowledge of danaine biology and literature; the personnel of the Dirección Nacional de Parques de la República Dominicana for their cooperation with logistics and permits; W. N. Ellis and T. Crosby for help with citations; and L. P. Brower, D. L. Gustafson, J. Miller, K. M. O'Neill and an anonymous reviewer for helpful reviews of drafts of this paper. This research was supported by NSF Grant DEB-9213266. This is contribution J-2978 of the Montana Agriculture Experiment Station.

LITERATURE CITED

- ACKERY, P. R. & R. I. VANE-WRIGHT. 1984. Milkweed butterflies: Their cladistics and biology. Cornell University Press, New York. 425 pp.
- ALAYO D. P. & L. R. HERNÁNDEZ. 1987. Atlas de las mariposas diurnas de Cuba (Lepidoptera: Rhopalocera). Editorial Científico-Técnica, La Habana, Cuba. 148 pp. & 49 plates.
- BELL, E. A. & J. J. DAYTON. 1986. Predation on monarch butterflies (*Danaus plexippus*) by chestnut-backed chickadees (*Parus rufescens*) at a California overwintering site. In Donahue, J. P. (ed.), Abstracts on the Second International Conference on the Monarch Butterfly (MONCON-2). 2-5 September 1986. Natural History Museum of Los Angeles County, Los Angeles, California. 21 pp.

- BOWERS, M. D. 1980. Unpalatability as a defense strategy of *Euphydryas phaeton* (Lepidoptera: Nymphalidae). *Evolution* 34:586-600.
- BOWERS, M. D., I. L. BROWN & D. WHEYE. 1985. Bird predation as a selective agent in a butterfly population. *Evolution* 39:93-103.
- BROWER, L. P. 1984. Chemical defence in butterflies, pp. 109-134. In Vane-Wright, R.I. & P. R. Ackery (eds.), *The Biology of Butterflies*, Symp. Roy. Entomol. Soc. London (1981). London.
- _____, & J. V. Z. BROWER. 1964. Birds, butterflies, and plant poisons: A study of ecological chemistry. *Zoologica* 49:137-159.
- _____, & W. H. CALVERT. 1985. Foraging dynamics of bird predators on overwintering monarch butterflies in Mexico. *Evolution* 39:852-868.
- _____, W. H. CALVERT, L. E. HEDRICK & J. CHRISTIAN. 1977. Biological observations on an overwintering colony of monarch butterflies (*Danaus plexippus*, Danaidae) in Mexico. *J. Lepid. Soc.* 31:232-242.
- _____, B. E. HORNER, M. M. MARTY, C. M. MOFFITT & B. VILLA-R. 1985. Mice (*Peromyscus maniculatus labecula*, *P. spicilegus*, and *Microtus mexicanus salvus*) as predators of overwintering monarch butterflies (*Danaus plexippus*) in Mexico. *Biotropica* 17:89-101.
- _____, M. A. IVIE, L. S. FINK, J. R. WATTS & R. A. MORANZ. 1992. Life history of *Anetia briarea* and its bearing on the evolutionary relationships of the Danainae (Lepidoptera: Nymphalidae). *Trop. Lepid.* 3:64-73.
- BROWN, K. S., JR. & J. VASCONCELLOS NETO. 1976. Predation on aposematic ithomiine butterflies by tanagers (*Pipraeidae melanonota*). *Biotropica* 8:136-141.
- CALVERT, W. H., S. B. MALCOLM, J. I. GLENDINNING, L. P. BROWER, M. P. ZALUCKI, T. VAN HOOK, J. B. ANDERSON & L. C. SNOOK. 1989. Conservation biology of monarch butterfly overwintering sites in Mexico. *Vida Sylvestre Neotropical* 2:38-48.
- CALVERT, W. H., W. ZUCHOWSKI & L. P. BROWER. 1983. The effect of rain, snow and freezing temperatures on overwintering monarch butterflies in Mexico. *Biotropica* 15:42-47.
- DAY, D. 1981. *The doomsday book of animals, an illustrated account of the fascinating creatures which the world will never see again*. The Viking Press, New York. 288 pp.
- DEAGAN, K. A. 1987. La Navidad, 1492, searching for Columbus's lost colony. *Nat. Geogr. Mag.* 172:672-675.
- _____. 1988. Archaeology of the Spanish contact period in the Caribbean. *J. World Prehistory* 2:187-233.
- DUFFEY, S. S. 1970. Cardiac glycosides and distastefulness: Some observations on the palatability spectrum of butterflies. *Science* 169:78-79.
- FINK, L. S. & L. P. BROWER. 1981. Birds can overcome the cardenolide defence of monarch butterflies in Mexico. *Nature* 291:67-70.
- HOWARTH, F. G. & G. W. RAMSAY. 1991. The conservation of island insects and their habitats. In Collins, N.M. & J. A. Thomas (eds.), *The conservation of insects and their habitats*. 15th Symposium of the Royal Entomological Society of London. Academic Press.
- ISHII, M. & H. MATSUKA. 1990. Overwintering aggregation of *Euploea* butterflies (Lepidoptera, Danaidae) in Taiwan. *Tyô to Ga* 41: 131-138.
- IVIE, M. A., T. K. PHILLIPS & K. A. JOHNSON. 1990. High altitude aggregations of *Anetia briarea* Godart on Hispaniola (Nymphalidae: Danainae). *J. Lepid. Soc.* 44: 209-214.
- KING, C. 1984. *Immigrant Killers. Introduced predators and the conservation of birds in New Zealand*. Oxford University Press, Oxford. 224 pp.
- KURLANSKY, M. 1992. *A continent of islands*. Addison Wesley, Reading, Massachusetts. 324 pp.
- KUSCHEL, G. 1987. The subfamily Molytinae (Coleoptera: Curculionidae): general notes and descriptions of new taxa from New Zealand and Chile. *N. Z. Entomol.* 9: 11-29.
- LLORENTE-BOUSQUETS, J., C. POZO-DE LA TIJERA & A. LUIS-MARTINEZ. 1993. *Anetia*

- thirza thirza* (Lepidoptera: Nymphalidae): su ciclo de vida y distribucion. Publ. Espec. Mus. Zool. (Universidad Nacional Autónoma de México) 7:63-87.
- MASTERS, A. R., S. B. MALCOLM & L. P. BROWER. 1988. Monarch butterfly (*Danaus plexippus*) thermoregulatory behavior and adaptations for overwintering in Mexico. Ecology 69:458-467.
- MOFFETT, M. W. 1991. Wetas - New Zealand's insect giants. Nat. Geogr. Mag. 180: 101-105.
- PARAMONOV, S. J. 1958. Lord Howe Island, a riddle of the Pacific. Pacif. Sci. 12:82-91.
- . 1963. Lord Howe Island. Pacif. Sci. 17:361-373.
- RILEY, N. D. 1975. A field guide to the butterflies of the West Indies. Collins, London. 224 pp.
- SAKAI, W. H. 1994. Avian predation on the monarch butterfly, *Danaus plexippus* (Nymphalidae: Danainae), at a California overwintering site. J. Lepid. Soc. 48: 148-156.
- SAS. 1990. SAS user's guide, Version 6.08, Cary, North Carolina.
- SCHWARTZ, A. 1989. The Butterflies of Hispaniola. University of Florida Press, Gainesville. 580 pp.
- SHAPIRO, A. M. 1974. Beak-mark frequency as an index of seasonal predation intensity on common butterflies. Am. Nat. 108:229-232.
- SMITH, D. A. S. 1979. The significance of beak marks on the wings of an aposematic, distasteful and polymorphic butterfly. Nature 281:215-216.
- SMITH, D. S., L. D. MILLER & J. Y. MILLER. 1994. The butterflies of the West Indies and South Florida. Oxford University Press, New York. 264 pp. + 32 plates.
- VANE-WRIGHT, R. I., P. R. ACKERY & T. TURNER. 1992. *Anetia jaegeri*, *Danaus cleophile* and *Lycorea cleobaea* from Jamaica (Nymphalidae: Danainae). J. Lepid. Soc. 46:273-279.
- VULINEC, K. 1990. Collective security: aggregation by insects as a defense, pp. 251-288. In Evans, D. L. & J. O. Schmidt (eds.), Insect defenses. Adaptive mechanisms and strategies of prey and predators. State University of New York Press, Albany.
- WANG, H. Y. & T. C. EMMEL. 1990. Migration and overwintering aggregations of nine danaine butterfly species in Taiwan (Nymphalidae). J. Lepid. Soc. 44:216-228.
- WATT, J. C. 1979. New Zealand Invertebrates, pp. 140-146. In Nature Conservation Council (eds.), A vanishing heritage: The problem of endangered species and their habitats. Nature Conservation Council, Wellington.
- WING, E. 1989. Human exploitation of animal resources in the Caribbean, pp. 137-152. In Woods, C. (ed.), Biogeography of the West Indies. Sandhill Crane Press, Gainesville.
- ZANONI, T. A. 1990. The flora and vegetation of Pico Duarte and Loma La Pelona, Dominican Republic—"The top of the Caribbean." Mem. New York Bot. Gard. 64: 279-289.

Received for publication 10 July 1994; revised and accepted 11 February 1995.